PSYCHE

Vol. 80 September, 1973 No. 3

THE EVOLUTION OF CRYPTIC POSTURES IN INSECTS, WITH SPECIAL REFERENCE TO SOME NEW GUINEA TETTIGONIIDS (ORTHOPTERA)*

By Michael H. Robinson

Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa Panama Canal Zone

Introduction

A number of authors (see, for instance, Cott 1940, and de Ruiter 1952) have suggested that the structural adaptations to defense by concealment that are found in insects can only function efficiently if they are accompanied by appropriate behavior patterns. These behavior patterns include diurnal immobility and the adoption of complex resting positions. A resting position may involve both the selection of an appropriate location (background selection) and the assumption of a special resting posture. The latter may entail systems that function to suppress signals that predators could use to locate the insect, and in addition may give rise to signals that convey false information about the edibility of the insect. The first category involves the strategy of concealment, the second category involves the strategy of mimicry.

I have suggested (Robinson 1968, 1969a, 1969b, 1973) that the protraction of the anterior legs of stick-mimicking insects (particularly phasmids and mantids, but including insects of other orders) in line with the long axis of the body has, *at the very least,* a dual function with respect to the signals that are potentially detectable by the predator. Thus, this behavior may:

(a). Conceal the legs, head and antennae of the insect, thereby suppressing signals that could be used as prey-detection cues by a predator.

*Manuscript received by the editor June 6, 1973.

(b). Enhance the general resemblance of the insect to a stick by increasing the apparent length of the body and providing it with a long tapering termination, thereby adding to the plant-part mimicry and signalling false information about edibility to (insectivorous) predators. Experiments that show that some predators can use the presence of heads and legs as prey-detection cues are described by Robinson (1973).

It seems probable that the behavioral and structural devices that serve to conceal prey-detection cues *and* also have a mimetic function evolved in the first place as part of a strategy of concealment and *then* constituted important steps towards the specializations involved in stick- or leaf-mimicry. Thus, for instance, insects that rest against a substrate can achieve maximum concealment by suppressing 'relief' or profile. This can be achieved by flattening or elongation, or both. Flattening could be a starting point for leaf-mimicry and elongation a starting point for stick-mimicry (examples in Robinson 1969b, but see also the recent careful study of Ghanian praying mantids by Edmunds 1972). Two examples of cryptic postures in tettigoniids from New Guinea are detailed in this paper. Both involve adaptations that are clearly related to concealment and at the same time dead-ends in the sense that they do not lie on the path to leaf-mimicry as it has been achieved in the orthoptera. Both adaptations are complex and interesting in themselves. Both involve the concealment of cue-structures and both involve profile reduction.

Materials and Methods

The insects were observed at the Wau Ecology Institute, Wau, Morobe District, New Guinea during the period April 1970 to April 1971, as part of a comprehensive study of insect anti-predator adaptations. This mainly involved the rich phasmid fauna of the area.[1] Both species were collected at night at the Institute and also at other localities in the Wau region. They were identified by Mrs. Judith Marshall of the British Museum (N.H.) London to whom the author is most grateful. Specimens are deposited with the Museum. Behavioral observations were carried out both in the field and in a large screened insectary. More than ten specimens of each species were examined.

[1]Observations made on more than thirty species of phasmid will be published as soon as the insects can be identified.

Figure 1. Dorsal view of *Acauloplacella immunis* in full cryptic posture on a leaf surface. Note the position of the legs and antennae and the fact that the head is largely tucked in under the prothorax. The lower anterior margins of the tegmina show the effects of this unusual tegminal position.

Description of Defensive Behavior

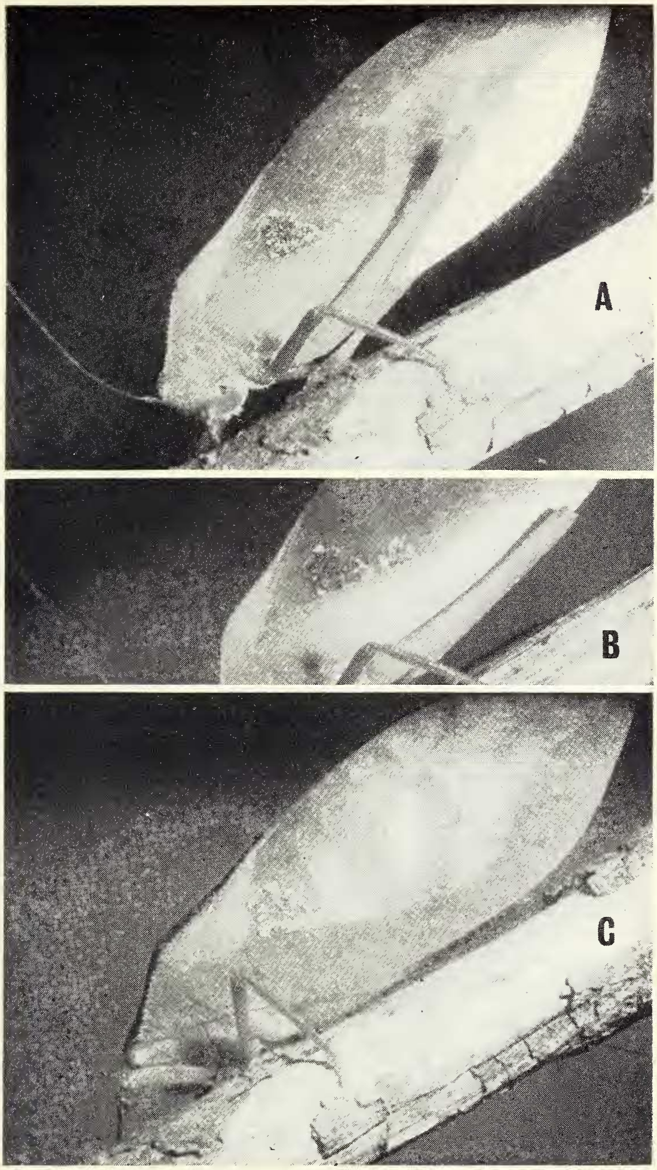
1. *Acauloplacella immunis* Brunner (Fam: Pseudophyllinae)

Specimens of this insect collected at Wau were a more-or-less uniform bright green in color. At night when actively moving about vegetation the insect looked like a 'typical' unspecialized tettigoniid. However by day the insect assumed a resting attitude on leaves (both upper and lower surfaces) that is shown in Figure 1.

This posture involves fairly complex changes in the orientation of the tegmina, the alignment of the legs and also in the relationship of the head, thorax and abdomen to the substrate. The change in the orientation of the tegmina is the most striking. Note, from Figure 1., that the tegmina are kept together at their posterior margins (which lie approximately in the midline of the body) and that their anterior margins (which lie lateral to the insect) are closely applied to the substrate. In the attitude of the active insect the angle between the contiguous tegmina is less than 90° (i.e. between their internal surfaces) while it becomes very obtuse (closer to 180°) in the flattened cryptic posture. In the cryptic posture the tegmina form a carapace-like structure that covers the second and third leg pairs. This change in the orientation of the tegmina is achieved by slow transition. In effect as the insect moves from a locomotory stance into its resting posture it lowers the body against the substrate, reorients the limbs, tucks the ventral part of the head beneath the prothorax and 'feathers' the tegmina outwards. In the resting posture the insect has a very low profile and the anterior legs are protracted side-by-side enclosing the antennae. The second and third leg pairs lie beneath the expanded tegmina: concealed completely or with part of the tarsi projecting.

It seems probable that in order to achieve this position the musculature of the tegminal base must be modified in some way and that each tegmen would exhibit some structural modification at its base. Perhaps some of the movements involved in stridulation require muscles and a form of tegminal articulation that facilitate the step to this form of profile concealment.

Figure 2. Stages A, B, and C in the assumption of the full cryptic posture (C) of *Phyllophora* sp. In A the major elements of the third leg are apposed and the leg is being moved towards the anterior margin of the left tegmen. In B the leg is about to be moved under the edge of the tegmen. In C the leg has been rotated at its base, moved under the tegmen and the tibia now lies closer to the midline of the body than the femur. Note the position of the head and antenna in the final stage.


A
B
C

2. *Phyllophora* sp. * (Fam: Phyllophorinae)

Specimens of this robust dark-green insect assumed diurnal resting attitudes on small branches. In the process the long third legs were folded at the femorotibial joint so that the tibia was closely apposed to the femur (inside edge to inside edge) and the apparent unit formed in this way was then tucked beneath the lower edge of the tented tegmen (its anatomically anterior margin). On one occasion when we filmed the process the insect brought first one tarsus forwards to the jaws, beneath the body, then the other. The tarsal region was groomed, in each case, and then the folding process was finished and the leg fitted into its cryptic stance. As the long hind legs are fitted into position beneath the tegmina the insect settles down so that its ventral surface is in contact with the substrate. At this stage legs I & II brace the resting insect. Interestingly enough the coloration of the outer margin of the tibia III was much paler (with pink overtones) than the rest of the joint. This coloration closely matches that of the ventral surface of the abdomen against which the folded unit is apposed. This coloration is visible only when the insect is viewed from below. Figure 2 shows the process of leg-folding and the final cryptic posture. We observed similar behavior in a very much larger phyllophorine that we did not collect.

Discussion

The *Phyllophora* sp. device can be regarded as primarily an adaptation for concealing the large ("characteristic") jumping legs of the orthopteran. This conclusion is based on comparison with functionally similar devices in other insects and is supported by the fact that the posture is adopted during the period of diurnal immobility when the insect is presumably at risk from visually hunting predators. On the other hand it is not a form of cryptic behavior consistent with the main line of evolution of leaf-mimicry in the Tettigoniidae. In that line leaf-mimicry has been achieved by flattening in the sagittal plane and reduction in the length of the tegmina (examples in Chopard 1938, Robinson 1969b).

The cryptic posture adopted by *Acauloplacella immunis* is a most interesting one in that it reduces profile and affords leg-concealment at the same time. It does not involve any marked dorso-ventral flattening in the active insect. It is an adaptation that is essentially more similar to the postural flattening of bark-living frogs and geckos (see Cott 1940) than other forms of crypsis found in the Orthoptera.

*Close to *P. cheesmanae* and *P. similis* de Jong.

Neither of the insects showed any of the forms of secondary defense that Robinson (1969a) suggested were consequences of escape-inhibiting cryptic postures. Both postures could be regarded as inhibiting the possibility of immediate escape following the penetration of the first line of defense. Thus in the *Phyllophora* position the jumping legs are in such a position that immediate escape by jumping is not possible although the animal *can* push itself off the substrate and drop. Similarly with *Acauloplacella*. Despite this neither animal had a startle display, chemical secretion or was armed with defensive spines.

Many of the orthopteroid insects that occur in this region of New Guinea have complex secondary defenses and in particular use strong spines in defense. This may be correlated with the fact that most of the mammalian predators of insects (marsupials) are nocturnal and handle their prey. They may thus be less susceptible to visual defenses and more affected by mechanical counter-attack.

References

Chopard, L.
1938. *La biologie des Orthoptères.* Paris: Lechavalier.

Cott, H. B.
1940. *Adaptive coloration in animals.* London: Methuen.

Edmunds, M.
1972. Defensive behaviour in Ghanian praying mantids. Zool. Journal Linnean Soc. London. 51: 1-32.

Robinson, M. H.
1968. The defensive behavior of *Pterinoxylus spinulosus* Redtenbacher, a winged stick insect from Panama. Psyche. 75: 195-207.
1969a. The defensive behaviour of some orthopteroid insects from Panama. Trans. Royal Entomological Soc. London. 121: 281-303.
1969b. Defenses against visually hunting predators. *In* Dobzhansky et al. Evolutionary Biology. 3: 225-259.
1973. Insect anti-predator adaptations and the behavior of predatory primates. Actas del IV Congresso Latinamericano de Zoologia II. 811-836.

Ruiter, L. de.
1952. Some experiments on the camouflage of stick caterpillars. Behaviour. 4: 222-232.